

Spatial variation of harmful algae and their toxins in flowing-water habitats: a theoretical exploration

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Flow in riverine reservoirs and impoundments can be strong enough to wash out phytoplankton populations, including harmful algae. However, fringing coves and shoreline features can comprise a hydraulic storage zone that enhances algal persistence. Mathematical models of this situation were constructed to represent populations of toxic flagellates or cyanobacteria, and complementary models represented dynamics of exchange between a single cove and a main lake. Steady-state analyses predict that spatial variation in algal abundance and toxin concentration along the axis of flow in a riverine reservoir is most likely to arise for critical flows just below those causing washout, which can be identified by the Péclet number. Spatial variation in algal abundance and toxin concentration between a single cove and the main lake is predicted to occur when a cove is hydraulically isolated from the main lake, or as a transient phenomenon during strong flow events. This modeling suggests a potential for managing harmful algal blooms through flow manipulations in some instances, or by localized controls of abundance or toxicity in relatively isolated coves.

KEYWORDS: harmful algal blooms; flow; reservoirs; hydraulic storage zone; flagellates; *Prymnesium parvum*; cyanobacteria; cylindrospermopsin

INTRODUCTION

Inland waters present a spectrum of flowing-water habitats that are inhabited to varying degrees by planktonic algae. In small, low-order streams with rapid currents, no true plankton develops and suspended algae arise transiently from the benthos. As order increases, and especially in broad rivers and riverine reservoirs, development of plankton becomes more likely. Nevertheless, the ecology of planktonic algae in flow-dominated systems has been somewhat neglected, and raises many paradoxes (Reynolds, 1990).

Among these is a basic question of persistence. Strong flow washes out populations of suspended algae

(Moustaka-Gouni *et al.*, 2006; Roelke *et al.*, 2010a), and continual strong flow can overwhelm the reproductive capacity of planktonic algae (Reynolds, 1990). A possible resolution of the persistence paradox lies in the complexity of the channel. There are many features along shorelines and on the bed that retard flow, producing slack regions and backwaters. These slow-flowing regions constitute a hydraulic storage zone that affects the downstream transport of suspended and dissolved constituents (Bencala and Walters, 1983; Martinez and Wise, 2003). Within such zones, the reproductive capacity of algae may be sufficient to permit population growth, even to bloom proportions.

Indeed, recent decades have seen the emergence of harmful algal blooms in high-order rivers and riverine reservoirs. For example, the haptophyte flagellate *Prymnesium parvum* was first documented to cause fish kills in the southwestern USA in a stretch of the Pecos River in Texas (James and De La Cruz, 1989). Since that event in 1985, blooms of *P. parvum* have occurred in several reservoirs along multiple rivers in Texas (Roelke *et al.*, 2010a, in press; Southard *et al.*, 2010). Blooms of several types of harmful algae have occurred in several other river, reservoir and estuary systems (Krogman *et al.*, 1986; Davis and Koop, 2006).

The occurrence of harmful algal blooms in riverine ecosystems demonstrates a viable phytoplankton community. In addition to a basic question of persistence in the presence of flow, other questions arise concerning the spatial variation of algal abundance and toxicity during bloom and flow events. Manipulation of flow is possible in some river systems, and has been suggested as a potential technique for managing and mitigating harmful algal blooms (Maier *et al.*, 2001; Mitrovic *et al.*, submitted for publication; Roelke *et al.*, 2010a). This possibility motivates the theoretical exploration of harmful algal dynamics in flowing conditions undertaken here. Another motivation lies in the fact that coves along the shoreline of riverine reservoirs might represent habitats where dynamics of harmful algae differ from the main reservoir. Such differences could perhaps also be exploited to mitigate harmful blooms and their effects.

This paper addresses two basic questions: What is the longitudinal distribution of algal abundance and toxicity under various flows, in a riverine reservoir? Secondly, what differences arise between a fringing cove and a main lake? For the first question, an idealized riverine reservoir was conceived in which a main channel with advective transport and dispersion was coupled to a hydraulic storage zone, representing an ensemble of fringing coves on the shoreline. Similar models are well developed for studying contaminant dynamics in flowing water systems, and were recently extended by the addition of algal populations (Grover *et al.*, 2009). As conceived here, this model of a riverine reservoir is best suited for understanding longitudinal patterns arising along the axis of flow. The second question addresses differences from the main reservoir arising in a single cove, rather than an ensemble. For this purpose, a simpler, two-compartment model of algal dynamics was constructed, in which one compartment is a small cove connected to a larger lake.

For both of these idealized habitats, models of algal and toxin dynamics were constructed, which deliberately simplified many of the complexities that pertain to harmful algae, with the goal of highlighting the role of

flow. There is a long history of modeling to study water quality problems relating to algae, especially eutrophication (Chapra, 1997). Some models treat space very simply and assume that there are one to three well-mixed zones, permitting considerable elaboration of biological and chemical kinetics (e.g. Park and Clough, 2004). Other models explicitly address one to three spatial dimensions, with sophisticated treatment of hydrodynamics at specific sites, although they sometimes less easily accommodate biological realism (Martin and McCutcheon, 1999). What is developed here occupies a middle ground. Biological processes essential to understanding harmful algae are incorporated, including population dynamics and toxin production and decay. The models are spatially explicit, but one-dimensional with simple habitat geometry and transport processes. A number of potential complications are neglected, including vertical stratification, light limitation and higher trophic levels. Such simplifications permit focusing on the role of one or a few key processes such as longitudinal flow and mode of toxin production.

In this study, steady-state analyses of the models constructed were complemented by examining event-driven dynamics using documented, extreme flow events from a riverine reservoir to force model output. Although the model structures are idealized, they support elaboration with details necessary for modeling specific systems, and although parameters are based on riverine reservoirs in Texas, USA, where harmful blooms have occurred, they could readily be changed to represent conditions found in other riverine systems worldwide.

METHOD

Physical settings

We developed spatially explicit models that approach the dynamic interactions of a main lake and its coves with two different idealizations. The first is a continuum approach using an advection–dispersion–reaction system to resolve transport and biochemical reaction kinetics along the main stem of a riverine reservoir. In this approach, an ensemble of fringing coves is represented as a hydraulic storage zone. The second approach focuses on a single cove that is coupled to a larger, main lake.

The continuum approach has one spatial dimension, the longitudinal axis (x) of a riverine reservoir from the headwaters ($x = 0$) to the dam ($x = L$) (Fig. 1, see Table I for notation). In the main, flowing channel of the reservoir, advection occurs at a rate v (m/day) and dispersion with coefficient δ (m²/day), which are constants unless otherwise specified. The main channel is

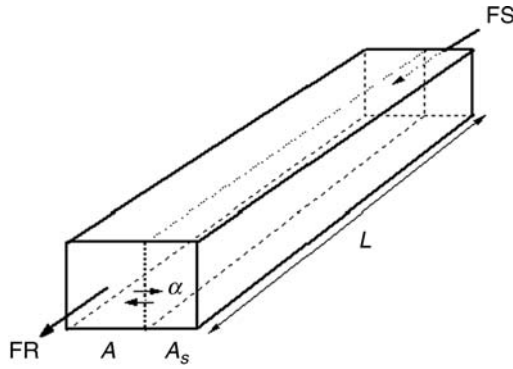


Fig. 1. One-dimensional representation of a riverine reservoir with a hydraulic storage zone composed of fringing coves and shoreline features.

Table I: Notation

Symbol	Meaning	Units
t	Time coordinate	Day
x	Space coordinate	m
$R(x, t)$	Nutrient concentration in main channel	$\mu\text{mol/L}$
$N(x, t)$	Algal abundance in main channel	cells/mL
$C(x, t)$	Toxin concentration in main channel	$\mu\text{g/L}$
$R_S(x, t)$	Nutrient concentration in storage zone	$\mu\text{mol/L}$
$N_S(x, t)$	Algal abundance in storage zone	cells/mL
$C_S(x, t)$	Toxin concentration in storage zone	$\mu\text{g/L}$
$R_1(t), R_2(t)$	Nutrient concentrations in main lake (1) and cove (2)	$\mu\text{mol/L}$
$N_1(t), N_2(t)$	Algal abundances in main lake (1) and cove (2)	cells/mL
$C_1(t), C_2(t)$	Toxin concentrations in main lake (1) and cove (2)	$\mu\text{g/L}$
L	Reservoir length	m
v	advection rate	m/day
δ	Dispersion coefficient	m^2/day
F	flow rate (discharge)	m^3/day
α	Exchange rate between main channel and storage zone	Day^{-1}
A	Cross-sectional area of main channel	m^2
A_S	Cross-sectional area of storage zone	m^2
V	Reservoir volume	m^3
D	Dilution rate	Day^{-1}
R_{in}	Nutrient supply to reservoir	$\mu\text{mol/L}$
ψ	Fraction of reservoir volume in cove	None
ϕ	Fraction of inflow entering cove	None
$R_1^{\text{in}}, R_2^{\text{in}}$	Nutrient supply to main lake (1) and cove (2)	$\mu\text{mol/L}$
E'	Volumetric exchange rate between main lake and cove	m^3/day
E	First-order exchange rate between main lake and cove	Day^{-1}
μ_{max}	Maximal growth rate of algae	Day^{-1}
K	Half-saturation constant for algal growth	$\mu\text{mol/L}$
M	Mortality rate of algae	Day^{-1}
ε	Toxin production coefficient	$\mu\text{g}/\text{cell}$ or none
K	First-order decay rate of toxin	Day^{-1}
q_N	Nutrient quota of algae	$\mu\text{mol}/\text{cell}$
q_C	Nutrient quota of toxin	$\mu\text{mol}/\mu\text{g}$
T	Temperature	$^{\circ}\text{C}$
Pe	Péclet number	None

connected to an ensemble of fringing coves treated as a hydraulic storage zone (Bencala and Walters, 1983), in which there is no longitudinal transport. At any point x along the length of the reservoir, there is exchange by Fickian diffusion between the main channel and storage zone at a rate α (day^{-1}). When the partial differential equations of the model are discretized for computation, the continuous storage zone becomes a series of coves of equal length. The cross section of the channel is partitioned into area A representing the main channel, and A_S representing the storage zone. Both cross sections are assumed to be invariant with length. Within both the main channel and the storage zone, algae grow and consume the limiting nutrient, while producing a toxin. Flow enters the headwaters at a rate F (m^3/day), carrying the limiting nutrient for algal growth at a concentration R_{in} ($\mu\text{mol/L}$), and a balancing flow exits at the dam, removing algae, nutrients and algal toxin. To simplify the model, constant reservoir volume V is assumed and the total system dilution rate is defined as $D = F/V$. To maintain water balance, the advection velocity v must then equal DL , where L is the reservoir length.

The second modeling approach focuses on a single cove, rather than a distributed ensemble, which undergoes Fickian exchange with a main lake (Fig. 2). A fraction ψ of the total system volume V occurs in the cove, and a fraction ϕ of the total inflow F goes into the cove. The same total flow F exits from the main lake. The limiting nutrient for algal growth enters the main lake at a concentration R_1^{in} and enters the cove at a concentration R_2^{in} . Water exchanges between the main lake and cove at a rate E' (m^3/day) and a net flow of ϕF also goes from the cove to the main lake to maintain constant volume. Flows of algae and algal toxin follow those of the nutrient. To simplify the model, constant volume was assumed, the system dilution rate was

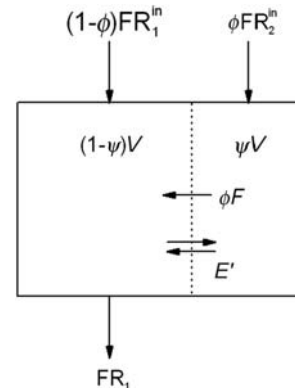


Fig. 2. Representation of a coupled cove—main lake system. Zone 1 on the left is the main lake, and zone 2 on the right is the cove.

defined as $D = F/V$ and the system exchange rate (day^{-1}) was defined as $E = E'/V$

Biological and chemical assumptions

For both modeling approaches, the same sets of assumptions were applied for algal population dynamics, and toxin production and decay. Algal growth is a Monod function of the limiting nutrient concentration (R) at a given location:

$$\mu(R) = \frac{\mu_{\max} R}{K + R} \quad (1)$$

with maximal growth rate μ_{\max} (day^{-1}) and half-saturation constant K (μM). Constant algal mortality is assumed at a rate m (day^{-1}). As algae grow, they consume nutrient with constant quota q_N ($\mu\text{mol}/\text{cell}$) and, for simplicity, the nutrient content of algae that die is instantaneously and locally recycled.

Three modes of production for dissolved toxins were explored. The first assumes that the rate of toxin production p ($\mu\text{g toxin L}^{-1} \text{day}^{-1}$) is proportional to the degree of algal nutrient limitation and to algal abundance, N (cells/L):

$$\varepsilon p(R, N) = \varepsilon(\mu_{\max} - \mu(R)N) = \varepsilon \left(\frac{\mu_{\max} K}{K + R} \right) N \quad (2)$$

where ε ($\mu\text{g toxin}/\text{cell}$) is a constant coefficient. We refer to this as the flagellate case, because some toxic flagellates such as *Prymnesium parvum* have been observed to produce toxins more rapidly when stressed by nutrient limitation (Johansson and Granéli, 1999; Granéli and Johansson, 2003; Chakraborty *et al.*, 2008; but see Lekan and Tomas, 2010).

The second mode of toxin production assumes that the rate of production is proportional to algal productivity, i.e. to the product of growth rate and abundance:

$$\varepsilon p(R, N) = \varepsilon \mu(R)N = \varepsilon \left(\frac{\mu_{\max} R}{K + R} \right) N \quad (3)$$

This case assumes that toxin is produced in proportion to other cellular products, and is then released to the water at a constant rate. We refer to this as the cylin-dropermopsin case, because it appears some producers of this toxin act in such a fashion (Hawkins *et al.*, 2001; Falconer and Humpage, 2006).

For simplicity, toxin degradation is assumed to follow first-order kinetics with a decay coefficient k (day^{-1}).

Governing equations

For the riverine reservoir model, the governing equation system is

$$\begin{aligned} \frac{\partial R}{\partial t} = & -DL \frac{\partial R}{\partial x} + \delta \frac{\partial^2 R}{\partial x^2} - (\mu(R) - m)Nq_N \\ & + \alpha(R_S - R) \end{aligned} \quad (4a)$$

$$\begin{aligned} \frac{\partial N}{\partial t} = & -DL \frac{\partial N}{\partial x} + \delta \frac{\partial^2 N}{\partial x^2} + (\mu(R) - m)N \\ & + \alpha(N_S - N) \end{aligned} \quad (4b)$$

$$\begin{aligned} \frac{\partial C}{\partial t} = & -DL \frac{\partial C}{\partial x} + \delta \frac{\partial^2 C}{\partial x^2} + \varepsilon p(R, N) - kC \\ & + \alpha(C_S - C) \end{aligned} \quad (4c)$$

$$\frac{\partial R_S}{\partial t} = -(\mu(R_S) - m)N_S q_N - \alpha \frac{A}{A_S} (R_S - R) \quad (4d)$$

$$\frac{\partial N_S}{\partial t} = (\mu(R_S) - m)N_S - \alpha \frac{A}{A_S} (N_S - N) \quad (4e)$$

$$\frac{\partial C_S}{\partial t} = \varepsilon p(R_S, N_S) - kC - \alpha \frac{A}{A_S} (C_S - C) \quad (4f)$$

with boundary conditions

$$\delta \frac{\partial R}{\partial x} \Big|_{x=0} - DLR(0, t) = -DLR_{\text{in}} \quad (5a)$$

$$\delta \frac{\partial N}{\partial x} \Big|_{x=0} - DLN(0, t) = 0 \quad (5b)$$

$$\delta \frac{\partial C}{\partial x} \Big|_{x=0} - DLC(0, t) = 0 \quad (5c)$$

$$\delta \frac{\partial R}{\partial x} \Big|_{x=L} = \delta \frac{\partial N}{\partial x} \Big|_{x=L} = \delta \frac{\partial C}{\partial x} \Big|_{x=L} = 0 \quad (5d)$$

where in the main flowing channel $R(x, t)$ is dissolved nutrient concentration at location x and time t , $N(x, t)$ is algal abundance at location x and time t and $C(x, t)$ is dissolved toxin concentration at location x and time t . The respective quantities in the hydraulic storage zone are denoted with a subscript S . Boundary condition (5a) specifies an inflow with nutrient concentration R_{in} , conditions (5b) and (5c) specify no inflowing algae or toxin and condition (5d) specifies that outflow occurs by advection only, as over a dam or weir.

Equation system (4) is appropriate when the toxin contains little or none of the limiting nutrient, which is true for many flagellate toxins (Murata and Yasumoto, 2000). In contrast, many cyanotoxins contain substantial amounts of nitrogen (Berry *et al.*, 2008), a potential

limiting nutrient. For N-limited cyanobacteria producing toxin in proportion to growth (cylindrospermopsin case), nutrient taken up from the medium is partitioned between cell production and toxin production, with ε being a dimensionless coefficient specifying the allocation to toxin production. The nutrient content of the toxin is designated q_C (mol nutrient/g toxin) and toxin degradation is assumed to recycle this content to dissolved nutrient. Dynamic mass balance for the nutrient then leads to these governing equations:

$$\frac{\partial R}{\partial t} = -DL \frac{\partial R}{\partial x} + \delta \frac{\partial^2 R}{\partial x^2} - (\mu(R) - m)Nq_N + kCq_C + \alpha(R_S - R) \quad (6a)$$

$$\frac{\partial N}{\partial t} = -DL \frac{\partial N}{\partial x} + \delta \frac{\partial^2 N}{\partial x^2} + [(1 - \varepsilon)\mu(R) - m]N + \alpha(N_S - N) \quad (6b)$$

$$\frac{\partial C}{\partial t} = -DL \frac{\partial C}{\partial x} + \delta \frac{\partial^2 C}{\partial x^2} + \varepsilon\mu(R) \frac{Nq_N}{q_C} - kC + \alpha(C_S - C) \quad (6c)$$

$$\frac{\partial R_S}{\partial t} = -(\mu(R_S) - m)N_Sq_N + kCq_C - \alpha \frac{A}{A_S}(R_S - R) \quad (6d)$$

$$\frac{\partial N_S}{\partial t} = [(1 - \varepsilon)\mu(R_S) - m]N_S - \alpha \frac{A}{A_S}(N_S - N) \quad (6e)$$

$$\frac{\partial C_S}{\partial t} = \varepsilon\mu(R_S) \frac{N_Sq_N}{q_C} - \alpha \frac{A}{A_S}(C_S - C) \quad (6f)$$

Boundary conditions (5) remain unchanged for equation system (6).

For the cove-main lake model, the governing equation system is

$$\frac{dR_1}{dt} = \frac{(1 - \phi)D}{1 - \psi} R_1^{\text{in}} - \frac{D + E}{1 - \psi} R_1 + \frac{\phi D + E}{1 - \psi} R_2 - (\mu(R_1) - m)N_1q_N \quad (7a)$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi} R_2^{\text{in}} + \frac{E}{\psi} R_1 - \frac{\phi D + E}{\psi} R_2 - (\mu(R_2) - m)N_2q_N \quad (7b)$$

$$\frac{dN_1}{dt} = -\frac{D + E}{1 - \psi} N_1 + \frac{\phi D + E}{1 - \psi} N_2 - (\mu(R_1) - m)N_1 \quad (7c)$$

$$\frac{dN_2}{dt} = \frac{E}{\psi} N_1 - \frac{\phi D + E}{\psi} N_2 - (\mu(R_2) - m)N_2 \quad (7d)$$

$$\frac{dC_1}{dt} = -\frac{D + E}{1 - \psi} C_1 + \frac{\phi D + E}{1 - \psi} C_2 + \varepsilon p(R_1, N_1) - kC_1 \quad (7e)$$

$$\frac{dC_2}{dt} = \frac{E}{\psi} C_1 - \frac{\phi D + E}{\psi} C_2 + \varepsilon p(R_2, N_2) - kC_2 \quad (7f)$$

where subscripts 1 and 2 denote quantities in the main lake and cove, respectively. Equation system (7) is appropriate when the toxin contains little or none of the limiting nutrient. For N-limited cyanobacteria producing toxin in proportion to growth (cylindrospermopsin case), dynamic mass balance for the nutrient requires these governing equations:

$$\frac{dR_1}{dt} = \frac{(1 - \phi)D}{1 - \psi} R_1^{\text{in}} - \frac{D + E}{1 - \psi} R_1 + \frac{\phi D + E}{1 - \psi} R_2 - (\mu(R_1) - m)N_1q_N + kC_1q_C \quad (8a)$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi} R_2^{\text{in}} + \frac{E}{\psi} R_1 - \frac{\phi D + E}{\psi} R_2 - (\mu(R_2) - m)N_2q_N + kC_2q_C \quad (8b)$$

$$\frac{dN_1}{dt} = -\frac{D + E}{1 - \psi} N_1 + \frac{\phi D + E}{1 - \psi} N_2 - [(1 - \varepsilon)\mu(R_1) - m]N_1 \quad (8c)$$

$$\frac{dN_2}{dt} = \frac{E}{\psi} N_1 - \frac{\phi D + E}{\psi} N_2 - [(1 - \varepsilon)\mu(R_2) - m]N_2 \quad (8d)$$

$$\frac{dC_1}{dt} = -\frac{D + E}{1 - \psi} C_1 + \frac{\phi D + E}{1 - \psi} C_2 + \varepsilon\mu(R_1) \frac{N_1q_N}{q_C} - kC_1 \quad (8e)$$

$$\frac{dC_2}{dt} = \frac{E}{\psi} C_1 - \frac{\phi D + E}{\psi} C_2 + \varepsilon\mu(R_2) \frac{N_2q_N}{q_C} - kC_2 \quad (8f)$$

Parameterization and numerical analysis

Biological parameters were assigned differing values for flagellates or cyanobacteria (Table II). Flagellates were assumed to be P-limited, while N-limitation was also considered for cyanobacteria. Parameter values are similar to those in previous models of flagellates and cyanobacteria in a Texas reservoir (Grover *et al.*, 2010). Algal mortality (m) was assigned a value of 0.1 day^{-1} , similar to the average value estimated for a Texas reservoir (Grover *et al.*, 2010). The first-order degradation rate for the algal toxin was assigned a value of 0.5 day^{-1} , corresponding to a half-life of 1.4 day, broadly consistent with observations of cyanotoxin degradation (Cousins *et al.*, 1996; Twist and Codd, 1997). For N-limited cyanobacteria, the parameter q_C was set to $0.001 \text{ } \mu\text{mol N}/\mu\text{g C}$, consistent with the stoichiometry of peptide cyanotoxins (Berry *et al.*, 2008).

For both the riverine reservoir and cove-main lake models, dilution rate D was set to 0.01 day^{-1} , near the average value for a Texas reservoir (Grover *et al.*, 2010). Assignments for the other physical parameters of the riverine reservoir model, which are likely highly variable, were arbitrary but within environmentally likely ranges: length $L = 10000 \text{ m}$; dispersion $\delta = 3 \times 10^5 \text{ m}^2/\text{day}$; storage zone exchange $\alpha = 0.5 \text{ day}^{-1}$; and cross-section ratio of main channel to storage zone $A:A_S = 4$. Likewise, assignments for the other physical parameters of the cove-main lake model were arbitrary within environmentally likely ranges: exchange rate $E = 0.3 \text{ day}^{-1}$; cove volume fraction $\psi = 0.01$; and cove flow fraction $\phi = 0.001$. For the riverine reservoir model, nutrient supply R_{in} was set to $1 \text{ } \mu\text{mol/L}$ for P-limited cases, and $20 \text{ } \mu\text{mol/L}$ for N-limited cases. For the cove-main lake model, nutrient supply to the main lake R_1^{in} was set to $0.5 \text{ } \mu\text{mol/L}$ for P-limited cases, and $10 \text{ } \mu\text{mol/L}$ for N-limited cases, while nutrient supply to the cove R_2^{in} was set to $1 \text{ } \mu\text{mol/L}$ for P-limited cases, and $20 \text{ } \mu\text{mol/L}$ for N-limited cases.

Many of the parameters were varied from these default values in sensitivity analyses focused on steady states. To explore non-steady dynamics under realistically variable flow conditions, daily dilution rates for Lake Granbury, Texas were estimated from 40-year

discharge histories of two gauges, as described previously (Grover *et al.*, 2010). The most extreme flow events were characterized by using dilution rate data from the wettest year on record, 1990, to force time-variable simulations of both models. Forcing data for this year were repeated until annually periodic dynamics emerged. To explore the influence of seasonal temperature variations on non-steady dynamics, a sinusoidal model was used to assign daily temperatures (T , °C) in a pattern consistent with observations of Texas reservoirs:

$$T = 20 + 10 \sin\left(\frac{2\pi t}{365} + 4.275\right) \quad (9)$$

Then, for every day, the algal maximal growth rate as a function of temperature $\mu_{\max}(T)$ was adjusted from the values in Table I, here denoted $\mu_{\max}(20)$, to indicate values at 20°C . For flagellates, the adjustment followed a unimodal function similar to that found by Baker *et al.* (Baker *et al.*, 2007) for *P. parvum*:

$$\mu_{\max}(T) = \mu_{\max}(20) \left[-0.1 + 1.07 \exp\left(1.86 \frac{T-20}{20}\right) - 0.26 \exp\left(3.72 \frac{T-20}{20}\right) \right] \quad (10)$$

For cyanobacteria, the adjustment followed a monotonically increasing function doubling the growth rate for a 10°C rise in temperature:

$$\mu_{\max}(T) = \mu_{\max}(20) \exp\left[\frac{\ln 2}{10}(T-20)\right] \quad (11)$$

Numerical analyses of the riverine reservoir model used the MacCormack algorithm (Chapra, 1997), with a discretization into 100 nodes of equal length. Numerical analyses of the cove-main lake models used a fourth/fifth order Runge–Kutta algorithm (Press *et al.*, 1986).

RESULTS

Extensive sensitivity analyses of the riverine reservoir model examined how parameter variations influenced the spatial patterns predicted at steady state. With other parameters at default values, physical parameters were varied through large ranges: dilution rate $D = 0.001 - 0.05 \text{ day}^{-1}$; dispersion $\delta = 3 \times 10^4$ to $3 \times 10^7 \text{ m}^2/\text{day}$; exchange rate $\alpha = 0.01$ to 10 d^{-1} ; and storage ratio $A:A_S = 0.01 - 100$. The development of longitudinal patterns at steady-state generally depended on flow

Table II: Biological parameters for models of harmful, toxin-producing algae

Parameter	P-limited flagellates	P-limited cyanobacteria	N-limited cyanobacteria
$\mu_{\max} (\text{day}^{-1})$	0.3	0.6	0.6
$K (\mu\text{mol/L})$	0.009	0.1	0.01
$q_N (\mu\text{mol/cell})$	1.39×10^{-9}	2.9×10^{-9}	32.5×10^{-9}
ε	$1.0 \times 10^{-8} \text{ } \mu\text{g/cell}$	$1.25 \times 10^{-8} \text{ } \mu\text{g/cell}$	0.00308

conditions, as summarized by the Péclet number

$$Pe = \frac{DL^2}{\delta} \quad (12)$$

with upstream–downstream gradients arising for Pe in a critical range of about 10–100. For higher values of Pe , algal populations were predicted to be washed out by rapid flow, but in this critical range downstream abundance was generally higher than upstream abundance (e.g. Figs 3 and 4). Under these critical flow conditions, predicted toxin concentration was higher downstream than upstream for flagellates (Fig. 3), but mid-reservoir peaks of toxin concentration were predicted for cylindrospermopsin producers for the critical Pe range (Fig. 4). Qualitatively similar results were found whether the critical range for Pe was accomplished by varying the dilution rate D or the dispersion δ .

In general, the steady-state differences between the storage zone and adjacent locations in the main channel were predicted to be small, for both algal abundance and toxin concentration. Under critical flow conditions producing upstream–downstream gradients, abundance and toxin concentration in upstream

locations were up to about 2-fold higher in the storage zone than the main channel (e.g. Fig. 5), but only if the exchange between these zones was very slow ($\alpha \leq 0.01 \text{ day}^{-1}$) or if the main channel was very small in relation to the storage zone ($A_1:A_S \leq 0.1$).

Examining steady states predicted by the cove-main lake model reinforces the conclusion that large differences between coves and a main lake arise only under restricted circumstances. Algal abundance and toxin concentration were predicted to be up to 40% higher in the cove than the main lake (Fig. 6). But differences exceeding about 10% arose only if the cove was relatively isolated from the main lake, with an exchange rate $< 0.01 \text{ day}^{-1}$, and had a nutrient supply concentration 10–20 times that of the main lake.

For both models, sensitivity analyses also explored steady-state predictions in response to changes in toxin production (ϵ) and decay (k) coefficients. Increasing the production coefficient or decreasing the decay coefficient always increased predicted toxin concentrations (with opposite results for opposite changes). However, even very large changes in these coefficients did not affect predicted spatial distributions, so results are not shown.

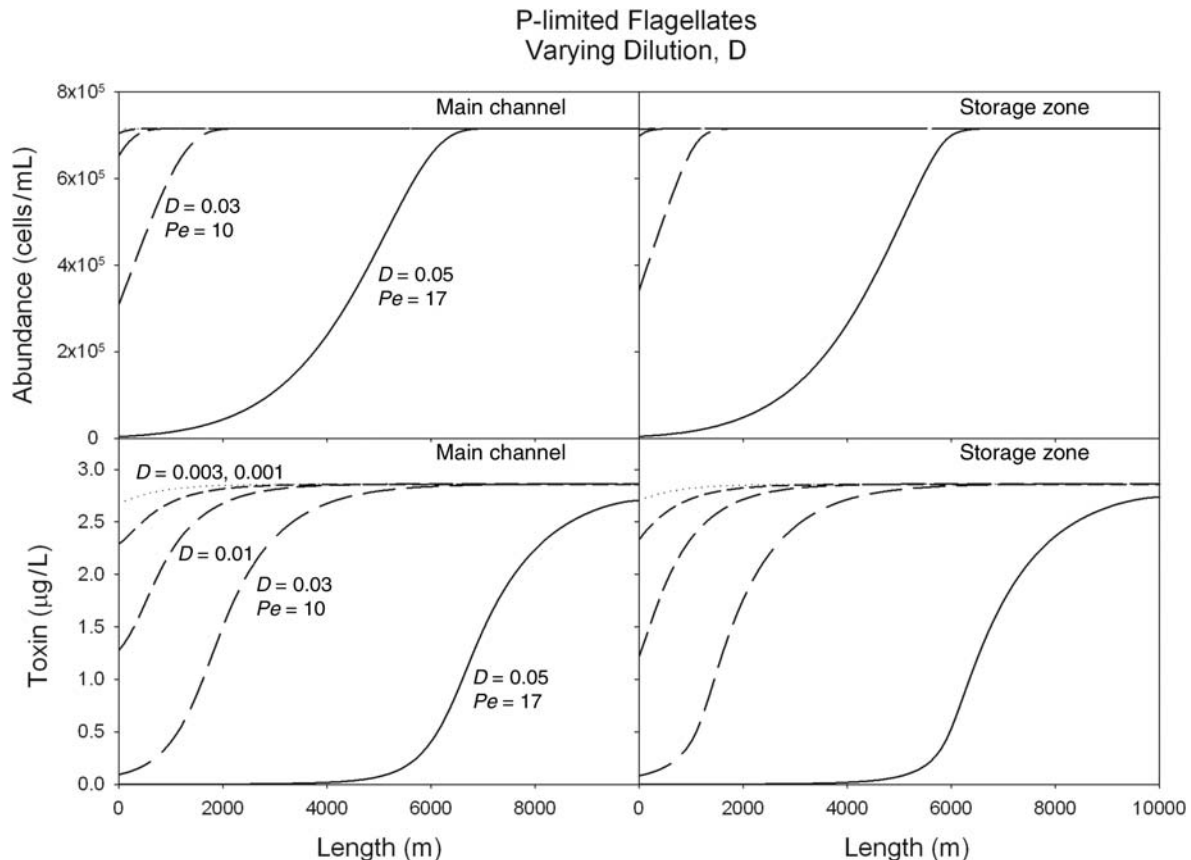


Fig. 3. Abundance and toxin concentration predicted by the riverine reservoir model at steady state for P-limited flagellates.

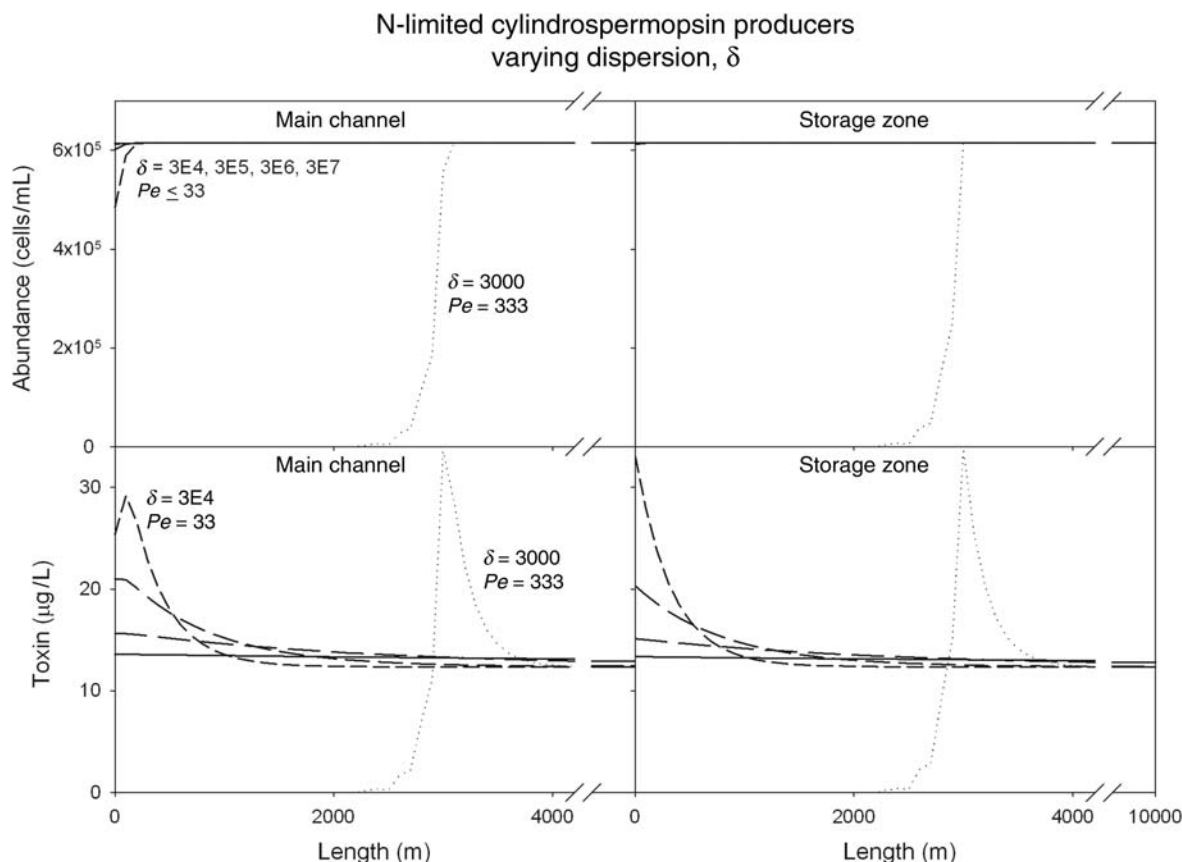


Fig. 4. Abundance and toxin concentration predicted by the riverine reservoir model at steady state for N-limited cylindrospermopsin producers.

Extreme flow events were predicted to have a strong influence on dynamics of harmful algae and their toxins, with washout occurring for dilution rates exceeding about 0.1 day^{-1} . Small residual algal populations permitted recovery from such events, but low abundance and lack of toxicity could persist several months past washout. For example, using dilution rates from a high flow year in Lake Granbury, Texas, P-limited flagellates suppressed by floods in late April did not recover their previous abundance until late November, and toxin concentration did not recover until December (Fig. 7). Adding temperature-dependent growth kinetics to the simulation shortened the predicted time to recover to August, because late summer–early autumn temperatures are similar to the modeled optimum for flagellate growth. Temperatures at this time increased the potential growth rate in relation to realized, nutrient-limited growth rate, and enhanced predicted toxin production by flagellates (Fig. 7, compare top and bottom panels). Spatially averaged abundance and toxin concentrations predicted for cyanobacteria were very similar to those shown for flagellates: spring flooding suppressed abundance and toxicity for weeks to

months, which were otherwise predicted to be high, and enhanced by high temperatures assumed to favor cyanobacterial growth (data not shown).

During periods of time with flows much lower than those high enough to wash out algal populations, the riverine reservoir model predicted that longitudinal distributions of abundance and toxin concentration would be near-uniform (e.g. Fig. 8). However, flows approaching those causing washout had Pe numbers in the critical range for producing longitudinal variations. In all cases, predicted transient distributions of algal abundance in the main channel and the storage zone during such critical flows resembled steady-state distributions, with low abundance upstream and higher abundance downstream (e.g. Fig. 8, around Day 80). Predicted toxin concentrations showed similar longitudinal distributions in response to flow variation for P-limited flagellates (Fig. 9). However, predicted toxin concentrations for cylindrospermopsin producers showed maxima in the upstream reaches for variable, but critical flow conditions (Fig. 10).

In all variable flow simulations, algal abundance and toxin concentrations were predicted to be similar in the

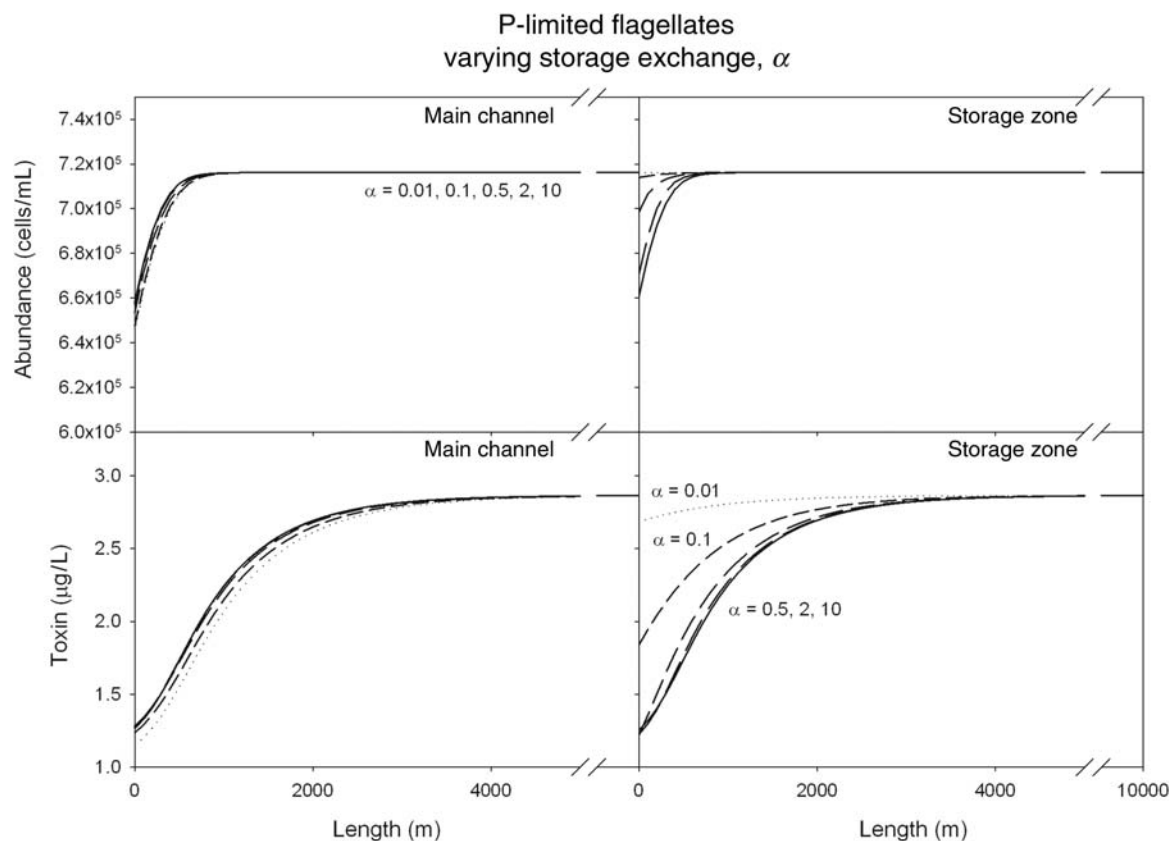


Fig. 5. Abundance and toxin concentration predicted by the riverine reservoir model at steady state for P-limited flagellates.

main channel and storage zone at most times (Figs 7–10). However, during high flows approaching or exceeding those producing washout, large transient differences were predicted in upstream reaches, with the storage zone having several fold larger algal abundance and toxin concentration than the main channel (Fig. 11).

Under most conditions explored, the cove-main lake model also predicted that a fringing cove would have similar algal abundance and toxin concentration to the main lake. Exceptions occurred on a transient basis in response to high flow, but only for coves that were relatively isolated from the main lake (with exchange rates \leq about 0.01 day^{-1}), receiving much higher nutrient supply (Fig. 12). The cove-main lake model was also less susceptible than the riverine reservoir model to washout and prolonged low algal populations during high flow events (e.g. compare Fig. 12 with Fig. 7).

DISCUSSION

This study examines the impact of flow on persistence of harmful planktonic algae, their accumulation to high abundance during blooms and the development of

toxicity in riverine habitats. Flow has long been recognized as important for planktonic dynamics in such habitats, and it has been suggested that hydraulic storage zones might be important in persistence and accumulation of phytoplankton in general (Reynolds, 1990). Formal modeling of that possibility is more recent, but has confirmed that hydraulic storage zones, such as those in the riverine reservoir model presented here, do contribute to persistence of planktonic algae (Grover *et al.*, 2009). The strong effect of flow on population dynamics of harmful algae has been confirmed by recent observations in riverine reservoirs (Roelke *et al.*, 2010a, in press). Flow events of the magnitude used in simulations presented here are strong enough to terminate blooms, and both observations and the modeling done here suggest that harmful algae remain sparse for weeks to months after such events.

This study also focused on the spatial patterns that develop in response to flow variation: longitudinal variations along the axis of flow, and differences between main channels where flow is strong and the fringing coves that compose the hydraulic storage zone. Steady-state models suggest some important principles. Longitudinal patterns are most likely to develop in a

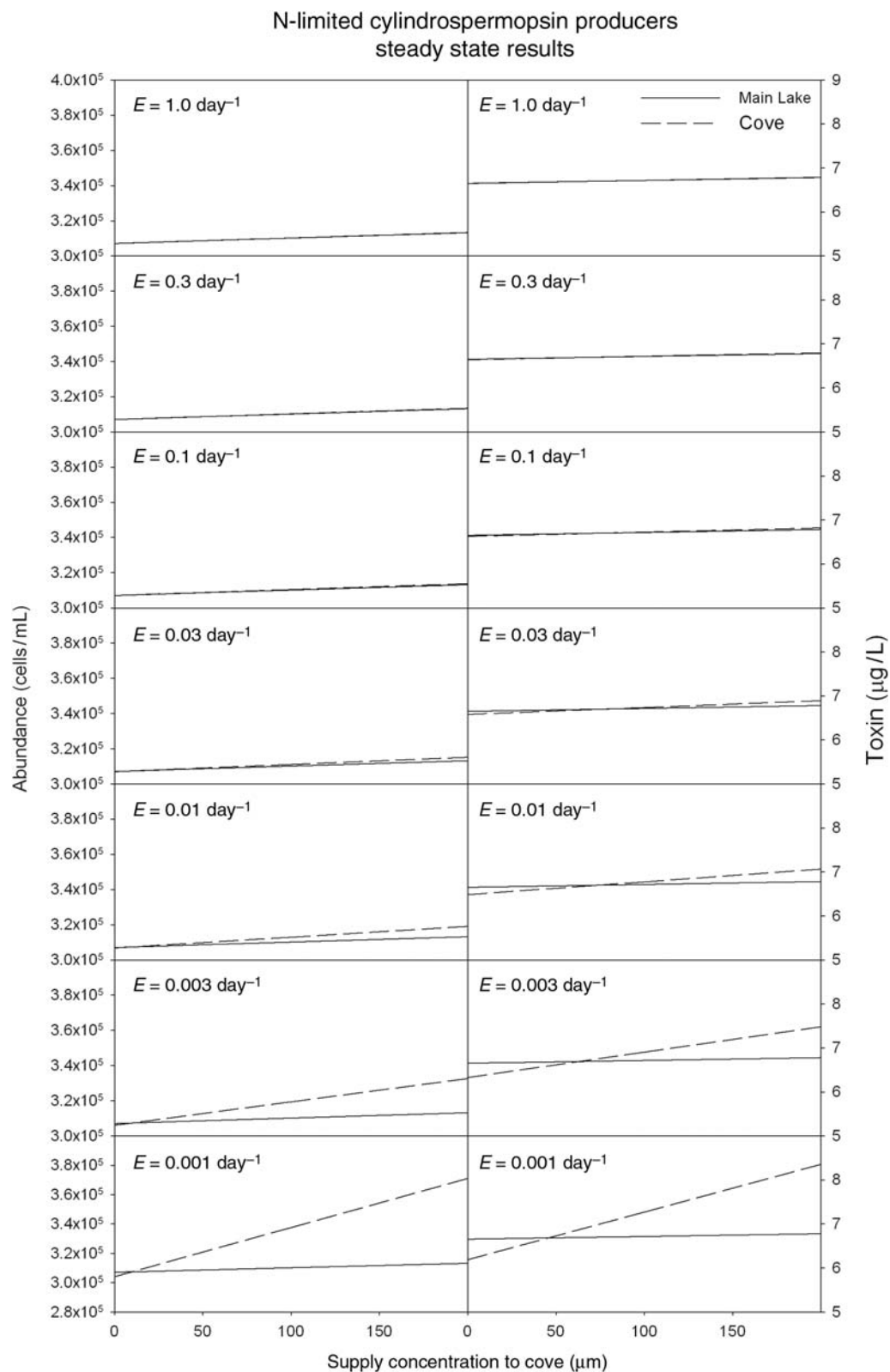


Fig. 6. Abundance and toxin concentration predicted by the cove-main lake model at steady state for N-limited cylindrospermopsin producers for varying exchange rates (E) and nutrient supply concentrations to the cove (R_2^{in}).

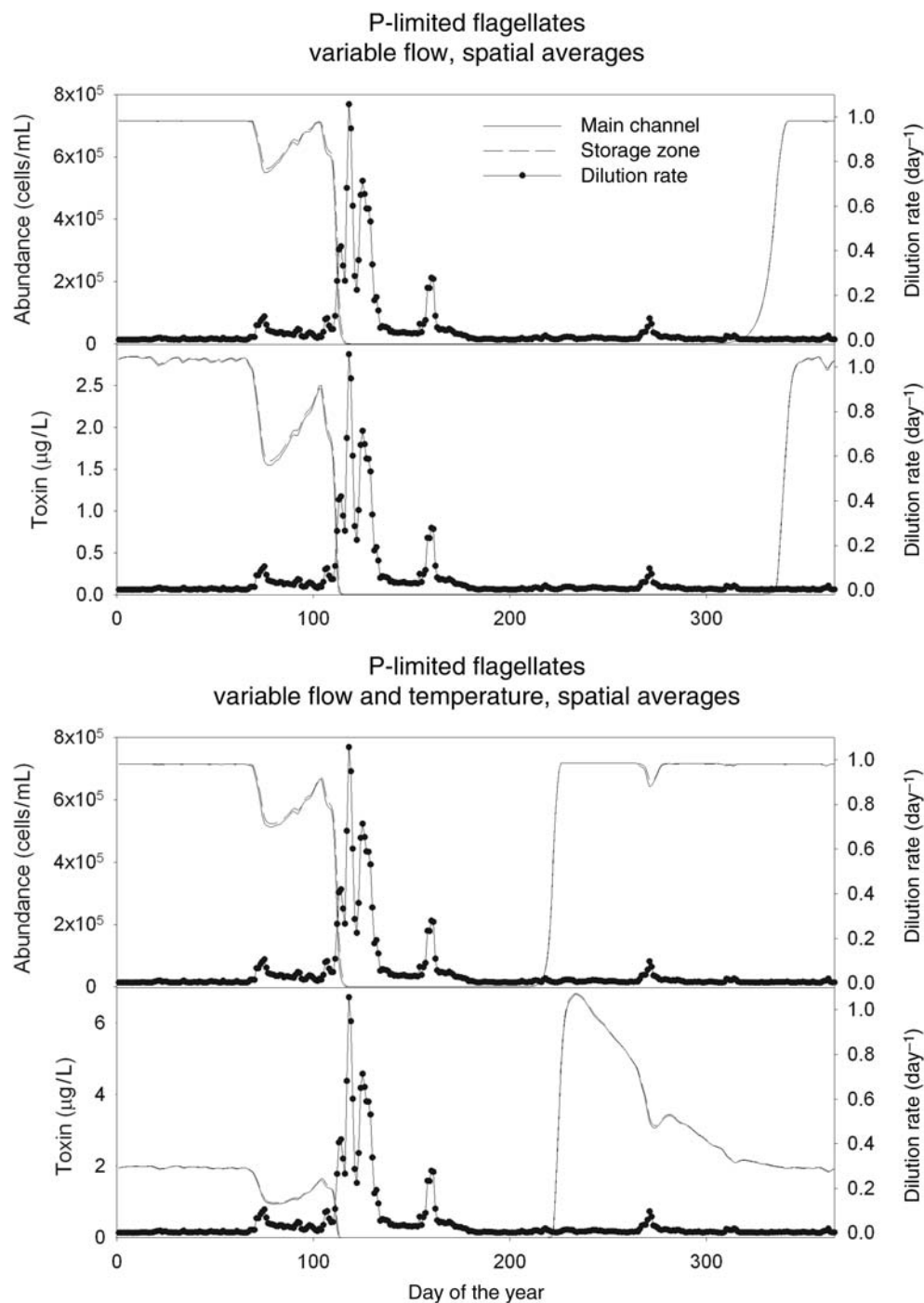


Fig. 7. Spatially averaged algal abundance and toxin concentration predicted by the riverine reservoir model in response to variable flow.

critical range of flows (identified by $Pe \approx 10-100$) just below those strong enough to wash out planktonic algae. Persistent differences between coves and the main channel are most likely to develop when coves have strong hydraulic isolation and high nutrient loading, and are located in upstream reaches.

The signatures of these steady-state patterns were partially maintained in dynamic simulations of variable flow. Strong longitudinal variations arose when flow events were in the critical range, and differences between coves and the main channel were often small. The most important qualification is that transient

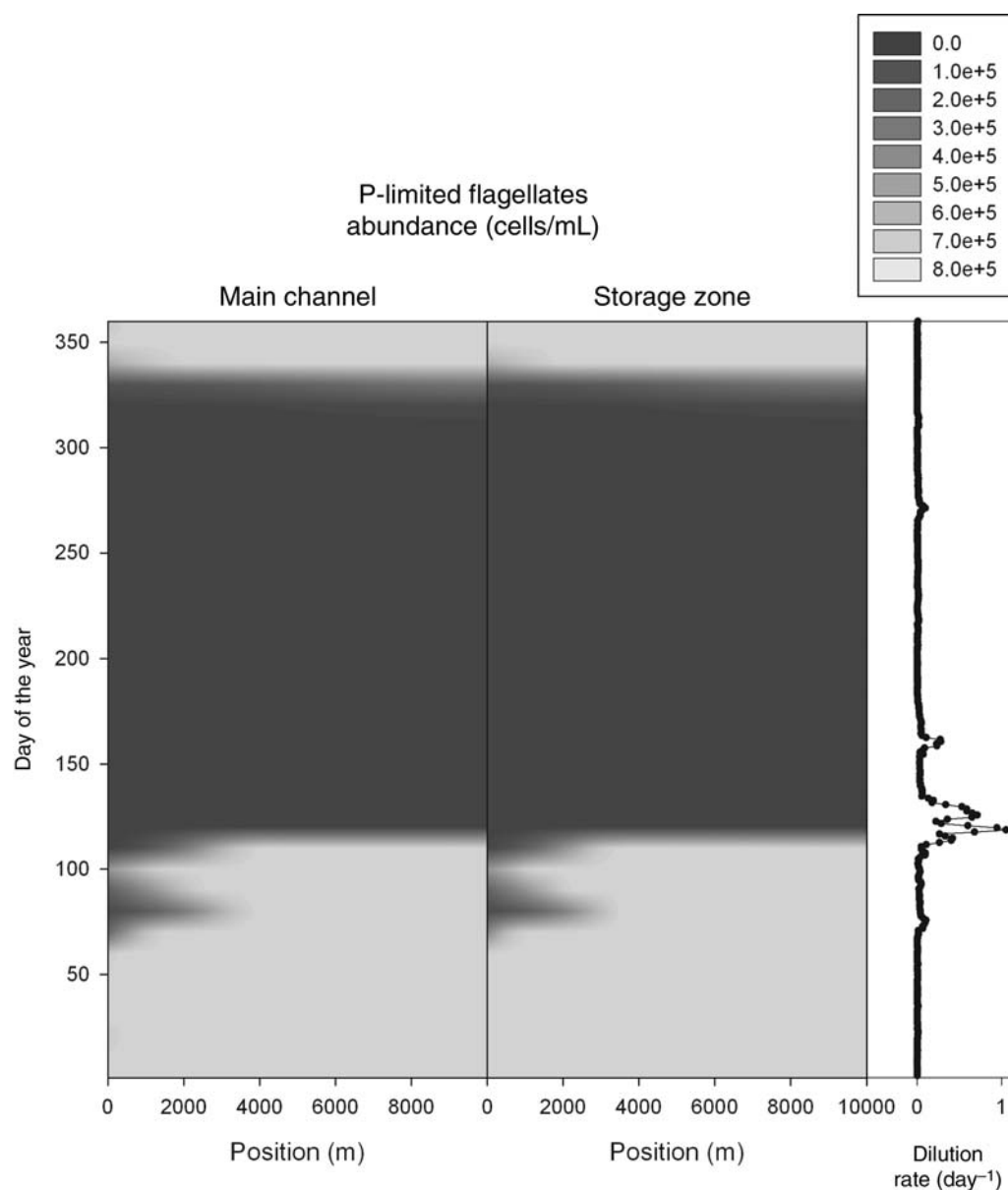


Fig. 8. Spatial distributions of algal abundance predicted by the riverine reservoir model in response to variable flow.

differences between coves and the main channel could be large in the aftermath of strong flow events. When high flows affect an established, toxic bloom, coves act as expected for hydraulic storage zones: algal abundance and toxin concentration remain high while washout occurs in the main channel. This retention of harmful algae and toxins is predicted to persist for tens of days during extended, high-flow events. Organisms moving to the slower waters of the hydraulic storage zone to avoid downstream transport in the main channel could suffer extended toxicity.

The spatial patterns predicted by this study should be testable with data that are often collected in riverine

reservoirs. For example, Roelke *et al.* (Roelke *et al.*, 2010a) documented the washout of a toxic bloom by a strong flow event. However, the spatial and temporal resolution of many monitoring programs might be too coarse to detect some of the predicted patterns. Transient patterns produced by the models presented here often lasted less than 1 month, but could persist for 7–10 days, and thus might be detected by weekly sampling. Ideally, spatial coverage would be synoptic. In cases where blooms are largely monospecific, continuous spatial sampling of *in vivo* chlorophyll (e.g. Roelke *et al.*, 2010a) would suffice to document the distribution of harmful algae.

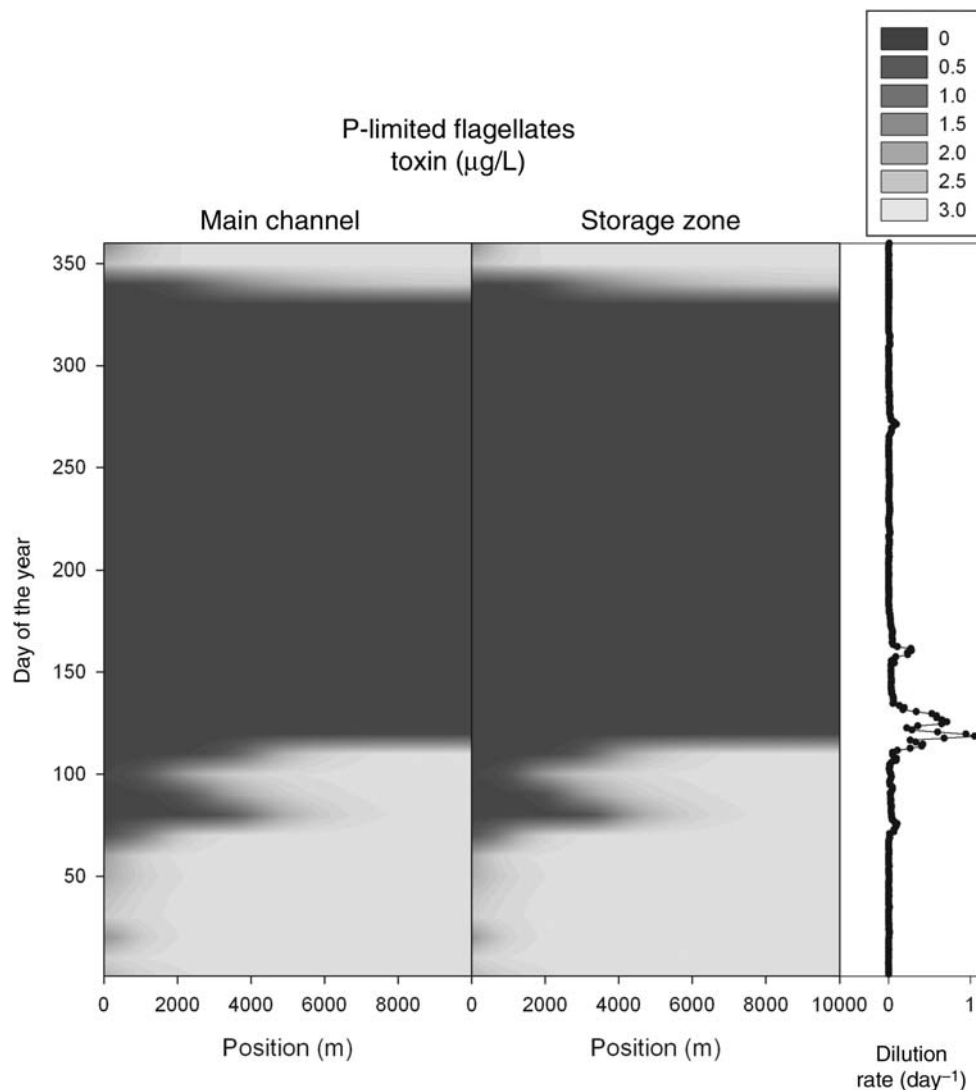


Fig. 9. Spatial distributions of toxin concentration predicted by the riverine reservoir model in response to variable flow.

In some reservoirs and other riverine habitats where toxic blooms have occurred, there might be opportunities to suppress blooms by controlled flow management (Maier *et al.*, 2001; Mitrovic *et al.*, 2003, submitted for publication; Roelke *et al.*, 2010a). Flow in many river systems is regulated, often to suppress flooding, which can have negative ecological consequences (Dewson *et al.*, 2007). Controlled flooding from upstream reservoirs could have benefits beyond suppressing harmful algae, such as restoring riparian vegetation (Stromberg *et al.*, 2007), and thus contribute to multiple objectives in the management of river ecosystems.

For large reservoirs prone to toxic, fish-killing blooms, such as those of *P. parvum*, smaller areas such as coves might be treated to suppress blooms or mitigate toxicity and provide a refuge for fish (Rodgers *et al.*,

2010; Roelke *et al.*, 2010c). The models examined here suggest that hydraulic isolation of coves will enhance such efforts. Coves often have short hydraulic residence times and relatively rapid exchange with the main lake body (Monismith *et al.*, 1990; James *et al.*, 1994). Treatment to mitigate toxic blooms could be ineffective unless a cove has an unusual degree of hydraulic isolation, or such isolation is effected with structures that impede flow.

Ecosystem management of harmful algae through enhanced flow or mitigation treatments within coves will carry costs and risks. It will be helpful to support any such effort with modeling. Ideally, models to support such management would be more sophisticated and tailored to specific sites than the generalized theoretical models presented here. These

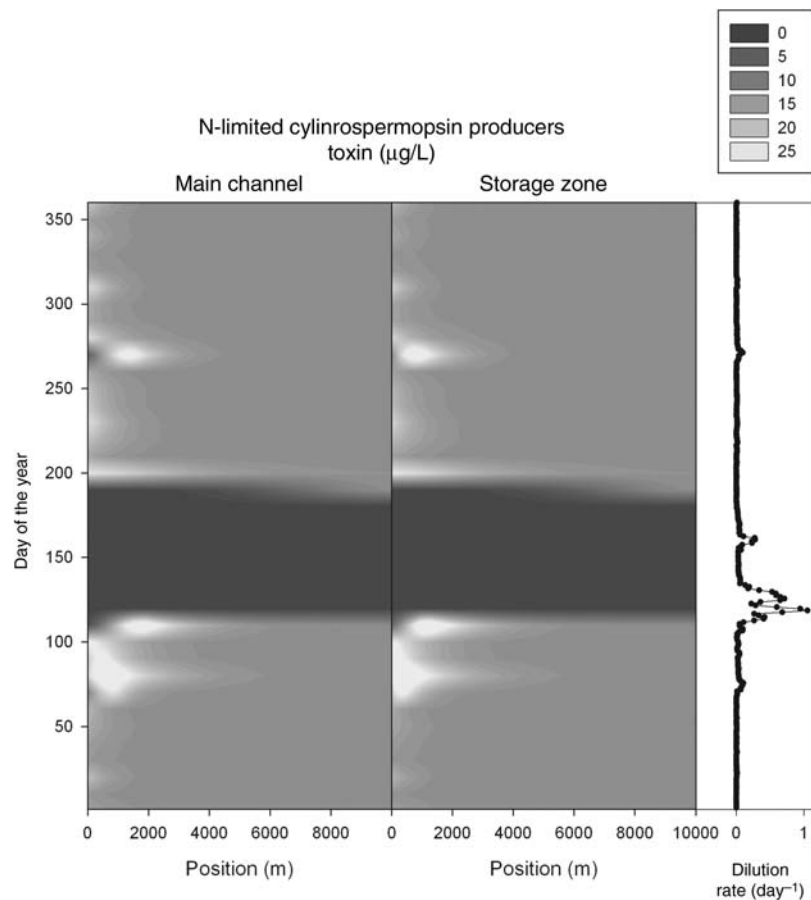


Fig. 10. Spatial distributions of toxin concentration predicted by the riverine reservoir model in response to variable flow.

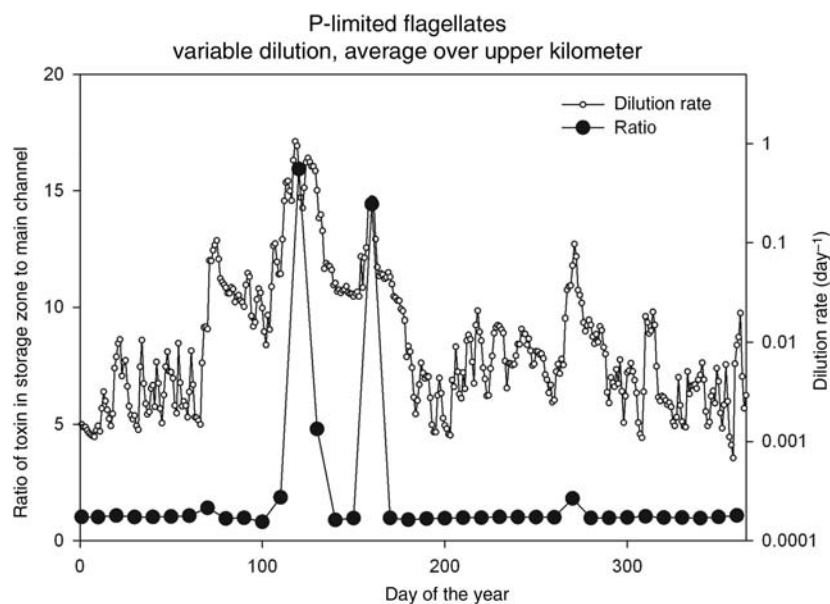


Fig. 11. Comparison of toxin concentrations predicted by the riverine reservoir model for the storage zone and the main channel in response to variable flow.

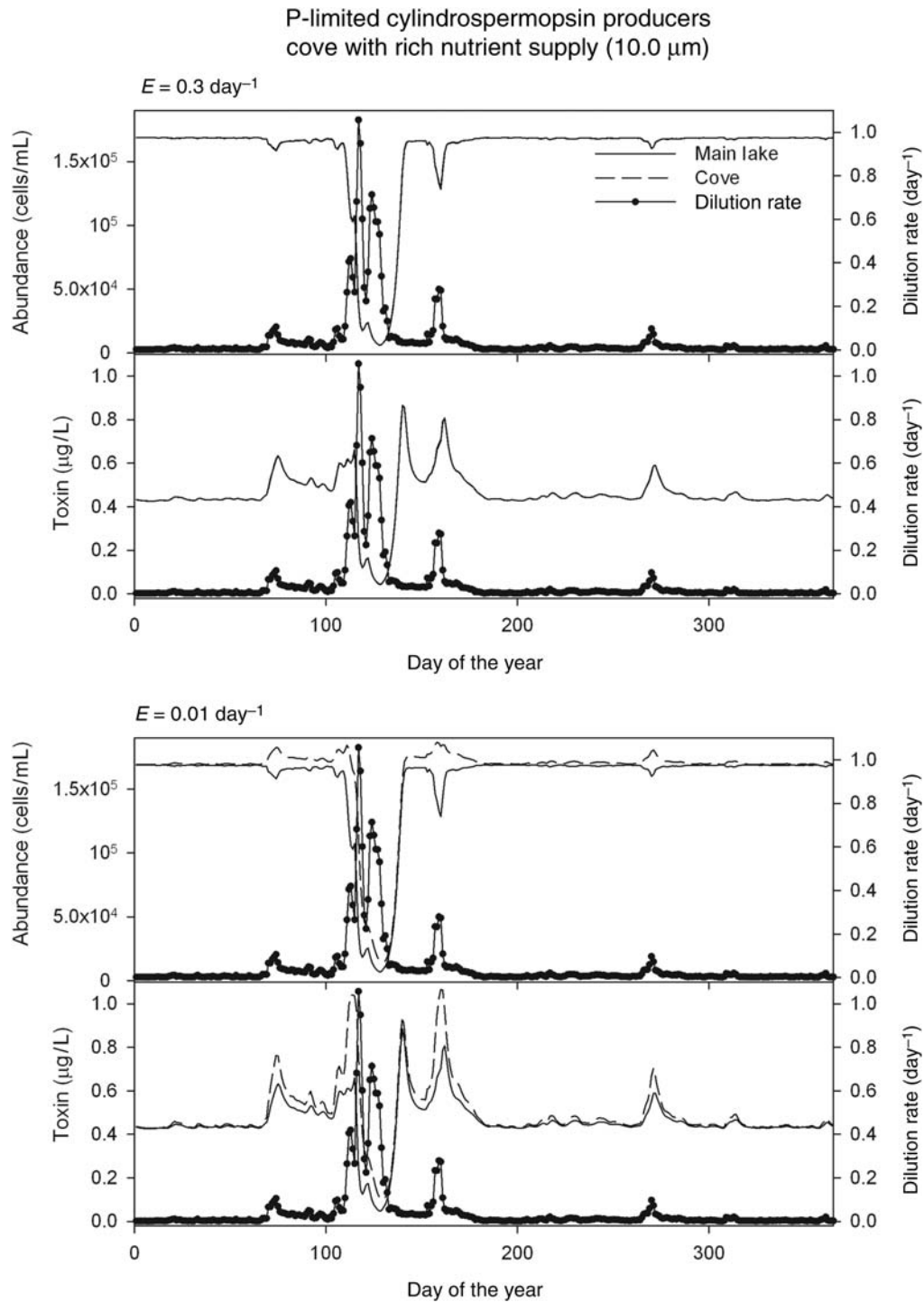


Fig. 12. Algal abundance and toxin concentration predicted by the cove-main lake model in response to variable flow.

models were deliberately simplified to have a minimally realistic portrayal of biological and physical processes, and explored in ways that emphasized the potential impact of flow. Necessary elaborations to support management decisions could include more

complete physical description, such as variable channel geometry, spatially varying advection and dispersion coefficients, and biological realism in the form of competitors, grazers and pathogens of harmful algae.

The simple models explored here neglect vertical variations and light limitation is not considered. Shallow, riverine reservoirs often have average irradiance above the likely limiting levels for algae (e.g. Grover *et al.*, 2010), though deeper reservoirs can display light limitation (Grover and Chrzanowski, 2004). Sediment loads associated with high flow events often reduce irradiance in such reservoirs, which could enhance the predicted suppression of harmful algae. Given the neglect of vertical variation and light limitation in the models studied here, they apply best to shallow systems that do not stratify. In deeper riverine systems, flow interacts with stratification to affect dynamics of algal blooms (Sherman *et al.*, 1998). Moreover, production and degradation of dissolved toxins are more complex than the simple idealizations considered here (e.g. Baker *et al.*, 2007; Preußel *et al.*, 2009). This study and others (Maier *et al.*, 2001; Roelke *et al.*, 2010a) suggest that flow manipulations can assist management of harmful algae in riverine systems, and provide a motivation for continued development of mathematical models.

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